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Spengelomenia, A new Genus of Solenogastres.

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With Plate 24–25.

During a recent trip to the Barbados Island I examined a small collection of alcyonarian corals that had been secured from a cable ship operating to the “northwest of the Florida coast”. Among these was a solitary specimen of solenogastre taken at a “depth of over a mile”. From the position of the animal it is not possible to decide whether it was originally attached to what is evidently a species of *Acanthogorgia*, or whether its lodgement in a mass of sponge and stony coral encrusting the base is accidental.

The animal measures 23 mm in length by 1,5 mm behind the head region where the diameter is greatest. From this point posteriorly the body gradually diminishes in size until the cloacal chamber is reached where the coelomoducts, their appendages and muscles produce a slight enlargement. The form of the head region is represented in Pl. 25 Fig. 13. Under low magnification the body has a spongy, reticulate appearance, the papillae occupying a somewhat sunken position corresponding to the meshes. The color in alcohol is light yellowish white.

The cuticle investing the body varies somewhat in height, but on the lateral and dorsal surfaces of the animal it measures approximately 0,12 mm in thickness. After decalcification it presents a decidedly shrunken appearance; and the papillae and the hypodermis

are unusually ill-defined and stain but faintly. A large number of cells, at least 50, compose the expanded portion of each papilla and a broad stalk attaches it to the hypodermis. Some of these cells of the expanded part, possibly all of them, contain a very few, light yellowish-brown granules.

The spines, forming several layers, are tangentially placed, but otherwise lie in every conceivable direction as they surround the papillae. While they differ considerably in size (0.04—0.16 mm) all agree in being hollow, somewhat curved with one end pointed and the other rounded.

The outlet of the anterior pedal gland (Pl. 24, Fig. 1, *pg*), separated from the atrial opening by a clearly defined spiculose tract, is unusually wide in transverse diameter, and the surface is further increased by the development of one great longitudinal fold on each side. In the opposite direction the diameter of the crypt is relatively short, and while the anterior wall is plain the posterior is produced into a few folds, three of which become continuous with the foot and a smaller fold on each side (Pl. 24, Fig. 9). It is possible that the depth of the outlet may vary considerably, the pressure of the somatic muscles on the blood contained in the visceral cavity producing a more or less complete eversion of the walls, while a pair of retractor muscles, inserted in the roof of the outlet and attached dorso-laterally to the body wall, doubtless produce an opposite effect.

The anterior pedal gland, whose cells contain an inky black secretion when treated with DELAFIELD'S haematoxylin, is a voluminous organ occupying a considerable portion of the visceral cavity between the front end of the brain and the level of the anterior end of the foot. Posteriorly its cells become reduced in size or the lobules contain fewer cells, and in this condition they merge insensibly into those of the posterior pedal gland. Anteriorly this last named organ is of more than average size, and the secretion escapes not only through the walls of the foot but through those of the two lateral folds (Pl. 24, Fig. 9). This state of affairs continues to the cloacal chamber where the foot enlarges slightly, and together with the lateral folds extends some distance on the large papilla bearing the external reproductive opening.

In several important respects the alimentary canal and its appendages bears a striking resemblance to what occurs in the genus *Alexandromenia*. The atrial opening, sub-terminal in position, leads

into a comparatively wide chamber whose walls are fashioned into the usual ridges enclosing the cirrose area. The inner ridge is somewhat obscured by a few adjoining folds that extend into the definite pharyngeal tube, but otherwise both it and the outer ridge are typical (Pl. 24, Fig. 1).

The opening from the atrium into the pharynx is comparatively wide, and the point of union is marked by the commencement of a set of glands that completely surround the digestive tube as far as the radula. Definite circular and longitudinal muscle sheaths likewise appear, and the epithelial lining becomes folded, the appearance in cross section bearing a strong resemblance, in this respect, to *Strophomenia*. A pair of strong retractor muscles attach to the body wall at the sides of the animal about the level of the posterior end of the radula, and on the other hand are inserted in the pharynx a short distance in front of the outlets of the ventral salivary glands.

The radula is well developed, is of the monoserial type and, judging from transverse sections alone, comprises 32 teeth. Each tooth (Pl. 25, Fig. 17) consists of a basal section from which, without any line of demarcation, two large triangular cusps arise. In turn each cusp bears from one to three needle-like processes, their form and number differing even on the cusps of the same tooth. In the angle between the cusps there is located a small, square or rectangular plate, apparently an expansion of the basal division, and this likewise bears small spines, somewhat variable in shape but invariably three in number. The direction of the sections renders it difficult to determine the number and arrangement of the odontoblasts, and this same difficulty is again met with in an attempt to reconstruct the slender radular muscles and the small spherical cells that apparently function as radular supports.

Up to the level of the radula the salivary glands present the form of small lobules, composed of small pyriform cells, closely packed together, their ductules opening by intercellular channels into the digestive tube. Beyond this point huge groups of pyriform cells, fashioned into globular lobules much as in the genus *Alexandromenia*, occur along the dorsal and lateral surfaces of the pharynx which in consequence is displaced far toward the ventral surface of the body. Fully a dozen pairs of these lobules are present, most if not, all of them apparently in communication with one of the two main, slender ducts coursing along the sides of the pharynx (Pl. 24, Fig. 1). In

cross section (Pl. 25, Fig. 21) a ridge may be seen to extend, like a typhlosole, along each canal. As in *Alexandromenia* neither of these canals opens directly into the pharynx but upon the summit of a small papilla that in turn is located at the bottom of a short tube opening on the side of the pharynx a little distance in front of the radula. Each papilla contains a few muscle fibres, and is probably capable in life of being projected through the pore directly into the pharynx.

Behind the radula the pharynx passes directly toward the ventral surface, and after reaching a level below that of the great salivary glands it turns abruptly backward and finally passes into the stomach-intestine. Throughout the first half of its course behind the radula its walls continue to be folded longitudinally, but beyond this point not only do the ridges disappear but the tube itself becomes exceedingly slender (Fig. 1). As in the genus *Alexandromenia* the posterior three fourths of the pharynx behind the radula is enveloped in numerous lobulated glands closely resembling those situated anterior to the radula, the chief difference being in the larger size of the lobules of the posterior set.

In its form and general relation to the other organs of the body the stomach-intestine is typical. A well developed anterior coecum is present, and sacculations, though not as clearly defined as usual, occur at fairly regular intervals, throughout the greater part of its course. Its epithelial lining, however, is uncommonly thick and the cells composing it are accordingly unusually slender, and furthermore are filled with some secretory product in the form of spherical granules of different sizes. Opposite the anterior end of the pericardium the gut becomes circular in outline, and as it rapidly narrows develops a few longitudinal folds that persist to the anal opening.

The hermaphrodite gland, extending from the head region to the pericardium, contains multitudes of spermatozoa and ova in an advanced stage of development. Masses of sperms occur in the spacious pericardial cavity, but as no trace of them is found in the adjoining section of the coelomoducts this is probably an abnormal state of affairs. The last named canals leave the pericardium as well defined structures, and enlarging but slightly, make their way forward to join the shell gland. Their walls throughout consist of columnar cells with basal nuclei, the remainder of the cell being filled with a faintly staining, almost homogeneous secretion that in

some parts of the duct has separated from the basal part. About midway between the pericardium and the shell gland are two small sacculations (Pl. 24, Fig. 12) that, since they contain spermatozoa, are probably seminal vesicles. It may be added that the sperms are not attached to the walls, but form a confused mass.

At the point of union of the dorsal section of the gonoduct with the ventral limb or shell gland on each side two short diverticula appear that present different appearances and probably perform different functions. The more posterior sac is identical with those just described and may be considered as a seminal vesicle, though like the one immediately in front it is empty. The anterior diverticulum is located in the usual position of a seminal receptacle, and furthermore resembles one in being attached to the shell gland by a short stalk, the opening into the expanded, distal portion being at the summit of a small papilla composed of slender columnar cells (Pl. 24, Fig. 11).

The shell gland consists of two distinct elements, (a) a slender tube, of somewhat larger calibre than the dorsal limb, composed of cubical or low columnar cells between which great numbers of (b) pyriform gland cells pour their secretion. This ventral tube runs parallel with the dorsal section, but is nearer the median plane of the body, and by a union with its fellow forms an undivided section opening into the cloaca. The gland cells form a dense envelop about each ventral duct from the undivided portion to a point about half way to the seminal receptacles where they disappear from the outer surface of the duct, but continue to be attached to its inner face throughout the remainder of their course. These glandular elements form small groups or lobules, their delicate ductules pursuing a course of varying length to the coelomoduct. The secretion they contain almost completely fills each cell in the form of a finely granular, moderately staining substance that accordingly renders them distinguishable from the mass of gland cells adjacent to the cloacal walls.

The terminal, undivided section of the coelomoducts is a simple tube, composed of slender columnar cells, that makes its way dorsally to open into the cloaca. Throughout its entire extent it is surrounded by a heavy sheath of circular muscles. As may be seen in Fig. 12, Pl. 24 the reproductive opening is borne on the summit of a great, flat-topped papilla whose muscular character and corrugated

walls suggest that in life it may, in the act of copulation, be extended beyond the cloacal opening.

Immediately behind the papilla bearing the reproductive opening the walls of the cloaca become developed into several large folds (Pl. 25 Fig. 16), filled with blood corpuscles, that thus probably serve as respiratory organs. Behind these, but not directly connected with them, is a slightly greater number of folds (Fig. 8), but in the present specimen they contain no blood corpuscles. A vast number of gland cells (Fig. 20), grouped into lobules, are situated in the visceral cavity between the posterior end of the pericardium and a point about level with the line I in Fig. 12, Pl. 24. They are more or less vacuolated and in a few cases appear to be pyriform (possibly due to pressure) but not a single, undoubted outlet for their secretion has been found. If they are not of the nature of plasma cells, related only to the blood streams in their midst, then their outlet is probably by intercellular channels into the cloacal chamber.

The circulatory system may be dismissed with a few words only as it presents no especially noteworthy features. The pericardium is of unusual size, but in the present specimen the heart is highly contracted and accordingly relatively small. As may be seen in Fig. 12 Pl. 24 the heart is free from the pericardial wall throughout the greater part of its course, and comprises two distinct divisions apparently guarded by a valve at the point of union. Into and out of the heart the blood follows the usual channels.

The nervous system, even as regards its broader features, is difficult to follow, owing chiefly to the fact that where the nerves or ganglia crowd their way between the glands and other organs they become so compact that they assume the appearance of muscle fibres. The results obtained are represented in Pl. 24 from which it may be seen that, with few exceptions, this system is similar to that of several other solenogastres. The three pairs of nerves passing out from the forward surface of the brain are typically disposed and distributed; and the three pairs of connectives are likewise normal. The ventral cords are connected as usual by commissures, and on the other hand are united with the lateral ganglia by connectives. One unusual feature presents itself in the form of a strong nerve that springs from the anterior end of each lateral ganglion and after branching repeatedly is distributed to the body wall. It is possible that some of its delicate branches pass over to the ganglia about the bases of the cirri, but generally speaking its subdivisions

become attached to the somatic muscles and in a few cases have been followed to the under surface of the hypodermis. A nerve from the anterior end of each ventral ganglion is likewise distributed to the ventral body wall but somewhat behind the one just described.

The labio-buccal connectives arise from the postero-ventral surface of the brain, and passing backward rest upon the pharyngeal glands. In this position they may be followed readily, but in the neighborhood of the ducts of the large, ventral salivary glands they disappear completely. In the neighborhood of the radula they once more come to view, and may be followed to the labio-buccal ganglia beneath the end of the radula sac. Before reaching these ganglia each connective becomes enlarged considerably and originates a nerve that in other species forms a dorsal connective, but in the present case such branches become very soon lost to sight among the numerous glands in the vicinity.

In the posterior end of the body the lateral and pedal cords continue to hold the usual positions, and here and there may be seen to be united by commissures and connectives. Opposite the posterior end of the pericardium the lateral ganglia expand somewhat and are united by a strong supra-rectal commissure. Posterior to this point they continue some distance and give rise to a few branches that appear to innervate the hypodermis and somatic musculature. As may be seen in Fig. 12 Pl. 24 the last two connectives uniting the ventral ganglia are relatively thick, and the same is true of the two most posterior commissures joining the ventral cords. These last named ganglia originate three or four large nerves that pass into the muscles composing the papilla supporting the reproductive opening, but they disappear almost immediately without giving any clue to their destination.

No dorso-terminal sense organ has been found to exist.

Concerning the relationships of this animal there is little to be said as it is not intimately related to any other known species. It readily comes within the family *Pruvotiniidae*, but here for the most part the problem of its more accurate systematic position must rest for the present. In a distant way there is a resemblance to the genus *Alexandromenia*. The radula is monoserial, and there are three sets of salivary glands, the most conspicuous, probably corresponding to the ventral in other molluscs, consisting of conspicuous lobules united to a long duct opening at the sides of the pharynx. The

heart is in part separated from the pericardial wall, and the ventral limbs of the coelomoducts are ensheathed in gland cells. These are the most obvious resemblances, and point to a community of descent, but beyond this point the question at the present time cannot be discussed with profit.

If it is difficult to frame anything approaching a convincing argument regarding the relationships of one genus, the matter becomes much more involved when the interrelationships of the entire order of solenogastres are concerned. With only a small number of genera known to the student of the group, and these usually clearly defined and not obviously related, most of the theorizing concerning their phylogenetic development must rest in large measure on personal opinion, and therefore is usually convincing only to its author. The same is true also in the discussion regarding the most archaic solenogastre or the most primitive mollusc. According to one investigator certain structures are declared to be primitive, and by another are considered to be coenogenetic. This is perhaps not a surprising state of affairs when we consider how far we are from possessing a broad and fundamental knowledge of the anatomy and embryology of molluscs, but it is to be hoped that especially in this last named field we may have more data to support our personal beliefs.

With the foregoing in mind I approach the subject of the primitive type of solenogastre in no dogmatic spirit, but after studying nearly fifty species of these animals certain facts have appeared that are suggestive. In another connection it has been argued (HEATH 1905), as other investigators have done, that the solenogastres appear to be more closely related to the chitons than to any other order. The symmetry of the body, the nature of the spines and their development, the snout and its innervation, the position of the heart, the relation of the aorta to the gonad and the head cavity, the relation of the pericardium and the coelomoducts, the two pairs of pedal glands and finally the nervous system are all fundamentally alike in the two groups.

Externally the individuals of the two orders differ much in appearance, but whether the worm-like solenogastre is primitive in this respect or whether it, like *Chitonellus*, has assumed this shape secondarily is not known. Among a few embryos of *Halomenia grandidata* in my possession are some advanced larvae that in form very closely resemble chiton embryos immediately before their meta-

morphosis, but neither these nor the ones described by Pruvot (1892) enable one to decide upon the form of body of the ancestral type. However it is important to note that in the young of *Halomenia* the anterior pedal gland, in process of formation, arises in the mid line behind the mouth as it does in the chiton embryo, and this suggests, though it does not prove conclusively, that formerly a creeping sole existed.

There has been considerable discussion regarding the subject of a foot in the solenogastres; whether the so-called ventral fold is the remnant of an ancient creeping surface or a late formation. In my opinion the ventral fold is a foot, and probably much reduced, as it has disappeared in the *Chaetodermatidae*; and that it is a foot is strongly supported by the fact that it is provided with two sets of glands, termed by HUBRECHT (1883) the anterior and posterior pedal, that are found in the chiton embryo. As I have shown (1911) the anterior pedal (the foot gland of KOWALEVSKI) disappears in the chitons at an early age, but before it vanishes it takes up a position similar to that in the solenogastres. In origin also the anterior pedal glands are similar in the chitons and the solenogastres. Finally there is a cleft in the heavy muscles of the ventral side in the mid line in the *Chaetodermatidae*, and all of these facts appear to me to indicate that the ventral fold is a foot, the remnant of a more fully developed one in the ancestral type.

NIERSTRASZ (1908, p. 250) has quoted me as making the claim that the "semicircular groove" is the equivalent of the outlet of the anterior pedal gland. What I have claimed is that in *Limifossor* there is a furrow (halbmondförmige Grube of Wiren) similar to the one found in *Chaetoderma* situated beneath the buccal sensory plate. It is lined throughout with the spiculose investment of the body, and to the base of it powerful muscles attach, and furthermore it is not the same as the cleft in the ventral somatic musculature. In other words I have not claimed that it is in any way related to the ventral groove in the *Neomeniidae*.

In some species of solenogastres several folds exist in addition to the usual median one, and in *Pachymenia abyssorum* there is a relatively broad creeping surface, but whether these are additional folds that have been secondarily derived from the outlying hypodermis, and whether in the second case the creeping surface has widened in comparatively recent times is not certain, but if this is

proved or disproved it does not necessarily throw any light on the point at issue.

About the shell there is nothing new to be said. It is absent in the present day species, and the imbricating chiton-like plates on the dorsal side of the larva may in reality be modified spines. In this connection it may be said that there is very little foundation so far as I can see, for the belief that the chitons (and the solenogastres if they are in reality of a common stock) have been derived from ancestors with a distinct head provided with tentacles, a highly arched visceral mass covered with a simple shell and posteriorly placed mantle cavity containing a small number of gills; and that in adapting themselves to a littoral habitat they have become transformed into the modern types. Comparative anatomy speaks in no certain tone regarding the subject, and embryology gives very little information indeed in support of such a belief. The very ill defined head the chiton possesses is even less evident in the larva; there is no indication of a visceral hump at any time; and in the formation of the mantle cavity there is no evidence whatever that it was originally located posteriorly, nor that it contained in the adults of a former period a small number of gills.

It has been asserted repeatedly that the branchial folds of the *Neomeniidae* are merely modified walls of the cloacal chamber, and that the plume-like gills of the *Chaetodermatidae* are but a further development and not therefore ctenidia. It is true that there are lamellae in both types of branchiae, and they are both placed in a cavity (that I believe to be a true mantle cavity at least in the *Chaetodermatidae*) at the posterior end of the body, but here the resemblance stops. The *Chaetoderma* type of gill is so remarkably similar to the generally recognized ctenidia of the prosobranchs or chitons for example that I cannot force myself to the belief that they have had a different phylogenetic origin. Whether the neomenian branchiae are a late development or not is far from being demonstrated, but to me their resemblance to ctenidia is not as close as some authors would have us believe.

As is well known it is exactly these external features that are the most readily modified, and are the ones most difficult to deal with. On the other hand the internal systems of organs, especially those comprising the nervous and coelom, are comparatively conservative and probably will afford the most fruitful field for the student of molluscan relationships. In fairly closely related groups

the digestive and circulatory systems are of value and may be compared in the case of the solenogastres and chitons with considerable profit. In another connection (HEATH, 1911) these have been discussed in considerable detail, and it is needless to rehearse the matter here.

In conclusion there is a word to say concerning the most primitive type of solenogastre, but here again there must, for the present, be differences of opinion. Not knowing the developmental history of any of these animals the difficulty is far greater than otherwise, since we cannot with even a fair degree of certainty differentiate primary and secondary features. It does seem however that in those species where the coelomoducts, in the adult condition, are comparatively plain and unmodified, and in this respect resemble the chitons, we are dealing with a primitive condition. In the young of several neomenians that I have examined, these structures likewise are relatively simple tubes, and I am strongly persuaded that when they appear in a fully developed condition provided with glandular appendages and penial spines and a relatively high degree of complexity they are not primitive species. Furthermore it frequently happens that this lack of simplicity in the posterior end of the body is correlated with a complex organisation in the anterior end. The basis for my belief is more or less intangible, but has resulted from the study of a comparatively large number of species, yet I cannot look upon *Neomenia* and *Alexandromenia* as primitive types. The genus *Spengelomenia* is accordingly one of the more specialized genera, and far removed from *Proneomenia* which to me appears to be one of the least modified genera.

The following diagnosis will distinguish the genus:

Spengelomenia n. g. Body worm-like, measuring 23 by 1.5 mm. Spicules slightly curved, needle-like. Papillae large, multinucleate. Three ventral folds. Gill folds 10—12. Numerous pharyngeal glands and enormous lobulate glands opening on sides of pharynx. Radula monoserial. Four pairs of vesicular appendages on dorsal limb of the coelomoduct; ventral limb surrounded in part by lobulated glands. Type of genus *S. bathybia* n. sp.

With character of the genus. Off the northeastern coast of Florida.

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Explanation of Plates.

Plate 24.

Fig. 1. Reconstruction of anterior end of *Spengelomenia bathybia*, showing brain and main nerves; the three sets of salivary glands, the globular lobules of one set being removed in part to show the main duct leading to outlet into pharynx. *gon* gonad. *pg* outlet of anterior pedal gland.

Fig. 2. Section through dorsal commissure and portion of pericardium (*p*) corresponding to line *H* in Pl. 24 Fig. 12. Under the nerve is the rectum beneath which is a portion of the cloaca, while the coelomoduct surrounded by circular muscles lies close to the ventral side. 50 : 1.

Fig. 3. Section along line *G*, Pl. 24 Fig. 12. The rectum is located beneath the pericardium (*p*) beneath which are the dorsal and ventral limbs of the coelomoducts, the latter surrounded by gland cells. 50 : 1.

Fig. 4. Section along line *B*, Pl. 24 Fig. 1 to show outlet from the ducts of the great lobulate ventral salivary glands. 50 : 1.

Fig. 5. Section along line *C*, Pl. 24 Fig. 1. The pharynx is surrounded by the lobules of the massive ventral salivary glands whose main ducts are lateral to the radula. 50 : 1.

Fig. 6. Section showing the cuticle, a papilla and the hypodermis. 330 : 1.

Fig. 7. Spines from side of body opposite front end of gonad. 330 : 1.

Fig. 8. Section through cloaca corresponding to line *J*, Pl. 24 Fig. 12. 50 : 1.

Fig. 9. Ventral folds, pedal glands and ventral nerve cords with commissure. 135 : 1.

Fig. 10. Section through posterior end of pharynx corresponding to line *D*, Pl. 24 Fig. 1. 24 : 1.

Fig. 11. Section corresponding to line *E*, Pl. 24 Fig. 12. Two lobes of the pericardium (*p*) adjoin the aorta; lateral to the stomach-intestine (*r*) are the coelomoducts, the one on the right showing the attachment of the seminal receptacle. 50:1.

Fig. 12. Reconstruction of posterior end of *S. bathybia*, showing pericardium, ganglia and principal nerves, coelomoducts with vesicular appendages and sheath of gland cells. The coelomoduct is represented as opening on the summit of a large papilla, into the cloaca.

Plate 25.

Fig. 13. *Spengelomenia bathybia*. $5\frac{1}{3}$:1.

Fig. 14. Section along line *F*, Pl. 24 Fig. 12, showing small, tubular heart, intestine beneath the pericardium and coelomoducts, the dorsal limb on right with diverticulum.

Fig. 15. Pharyngeal glands between brain and radula. 230:1.

Fig. 16. Section through cloacal cavity, corresponding to line *I*, Pl. 24 Fig. 12.

Fig. 17. Portion of radula. 230:1.

Fig. 18. Glands from pharynx behind the radula. 91:1.

Fig. 19. Section through atrial cavity, corresponding to line *A*, Pl. 24 Fig. 1.

Fig. 20. Section through external reproductive opening on summit of papilla in cloacal cavity that is surrounded by numerous glands.

Fig. 21. Section through one of the ventral salivary gland lobules and duct. 91:1.

Fig. 22. Blood corpuscles. 555:1.